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# STUDIES ON THE EMBRYOLOGY AND RELATIONSHIPS OF SOUTH AFRICAN GENERA OF THE HAEMODORACEAE: LANARIA AIT.

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## ABSTRACT

The embryological development of *Lanaria plumosa* is given. It shows a greater similarity to that of genera of the Tecophilaeaceae of Hutchinson's system than to the Haemodoreae or the Conostyleae, the tribes to which *Lanaria* has been assigned by various taxonomists. This suggests that the position of this monotypic genus in present taxonomic systems is probably not correct and that it stands closer to the Tecophilaeaceae than to the Haemodoreae or the Conostyleae.

## SAMEVATTING

Embriologiese ondersoek by die monotipiese endemiese *Lanaria plumosa* toon dat die selwande van die jong stuifmeelkorrels gelyktydig aangelê word. Die generatiewe sel word proksimaal aangelê in die stuifmeelkorrel. Die helmknop het 'n gewone sekresietapetum.

Twee anatrope saadknoppe in apotrope posisie is in elke vrugbeginselhok aanwesig, elk met twee integumente en 'n klein obturator aan die basis. Die buitenste integument is dik en die mikropiel word deur beide gevorm.

'n Dek-sel word van die sub-epidermale archesporiumsel afgesny. 'n Ry van vier makrospore ontstaan, en die basale een ontwikkel op die normale wyse tot kiemsak.

Onder die mikropiel vergroot die nucellus deur peri- en antiklinale seldelings van die dek-sel en die nucellusepidermisselle. Later word meeste van die nucellus geresorbeer, behalwe vir die weefsel aan die basis.

Die endospermontwikkeling is heelwaarskynlik helobiaal. Die klein basale endospermkamer het verskeie kerne maar vorm nie 'n haustorium nie. Uit die boonste kamer ontstaan die endospermweefsel, na 'n groot aantal vrye kerne eers gevorm is.

Uit 'n lineêre viersellige pro-embrio ontstaan die gedifferensieerde embrio, in alleen één van die ses saadknoppe. Die saadhuid word van beide integumente gevorm, maar oorweënd van die buitenste.

Die embriologiese kenmerke van *Lanaria* stem beter ooreen met die van die Tecophilaeaceae as met die Haemodoreae of die Conostyleae—die twee tribusse waarin *Lanaria* tot dusver geplaas was. Hierdie ondersoek toon dus dat die sistematiese posisie van *Lanaria* waarskynlik nie reg is nie, en dat dit nader verwant is aan die Tecophilaeaceae.

## INTRODUCTION

*Lanaria*, a monotypic genus with one species, *L. plumosa* Ait., is localized in the south coast districts of the Cape Province, from Somerset West to Albany. It is distinguished by regular trimerous flowers with six stamens and a semi-inferior ovary, the whole flower and also the inflorescence being densely covered with long white plumose hairs.

Taxonomists have differed about its systematic position. Bentham & Hooker (1883) place it in the Haemodoraceae, tribe Euhaemodoreae, together with nine other genera, three of which, *Wachendorfia*, *Dilatris* and *Barberetta*, are endemic in South Africa, two in Australia and the other four in the Americas.

Pax (1930) in Engler and Prantl's work, reduces the Haemodoraceae to a small family characterised by three stamens opposite the inner perianth segments. The family is thus limited to eight genera of Bentham and Hooker's Euhaemodoreae, and the genus *Pauridia*. On account of their six stamens the genera *Lanaria* and *Phlebocarya* are transferred to the Conostylideae, and this tribe to the Amaryllidaceae subfamily Hypoxidoideae.

Hutchinson (1944), on the other hand, again transfers the Conostyleae to the Haemodoraceae which then consists of the two tribes Conostyleae and Haemodoreae (i.e. Euhaemodoreae of Bentham and Hooker). At the same time he returns *Lanaria* and *Phlebocarya* to the tribe Haemodoreae where Bentham and Hooker had placed it. This tribe is then characterised by the possession of three or six stamens, a very short or no perianth tube, and 2-seriate perianth segments. In the Conostyleae the perianth tube is often fairly long and curved and the segments are l-seriate and subvalvate.

In an attempt to determine the relationships of *Lanaria* more precisely, its embryological development has been investigated and compared with that of other related genera. The results are given below.

## INVESTIGATION

*Material and Method.* Young flower buds and older stages of the flowers of *Lanaria plumosa* obtained from the Caledon Division, were fixed in FAA. It was necessary to dissect older ovules out of the ovaries, as the hairy ovary walls hindered sectioning. After embedding in paraffin wax the material was cut 12—15 $\mu$ in thickness and stained either with Delafield's or with Heidenhain's haematoxylin, the latter frequently used in combination with fast green.

*Pollen.*—The reduction division in the anthers occurs at about the time when a parietal cell is cut off in the young ovule. The formation of cell walls in the pollen mother cells is simultaneous, occurring after the second reduction division. The generative cell of the pollen grain is more or less spindle-shaped and is formed against the proximal cell wall, i.e. opposite the groove (Figs. 18, 19).

No periplasmodium is formed in the anthers and the tapetum is a secretion tapetum which is still to be seen as a well-developed layer of the anther wall at the time when the young pollen grains are freed from the walls of the pollen mother cells. The tapetal cells become two- or more-nucleate but later the nuclei usually fuse to form large polyploid nuclei.

*Position and form of ovule.* The ovary, which is nearly completely inferior, has a conical tip protruding for a short distance into the perianth tube. It is trilocular and has two anatropous ovules placed side by side in each chamber, one ovule occasionally slightly higher than the other. From the small axile placenta situated near the base of each chamber, the two very short funiculi ascend, and the ovules are placed with their micropyles pointing downwards and outwards (Figs. 1, 7), i.e. their position is apotropous.

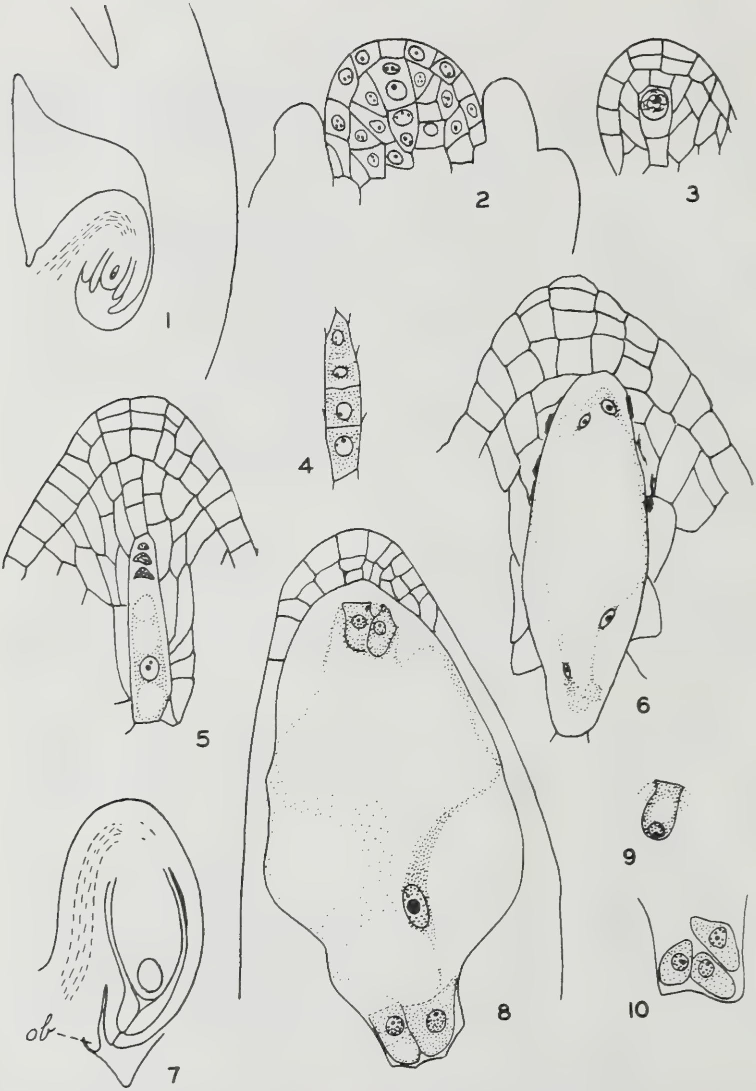
A small protuberance develops from the base of the funiculus (Fig. 7). Although slightly smaller, it is comparable to the obturator described by Cave (1952) in *Odontostomum.* It has papillose epidermal cells, rich in protoplasmic contents.

*Integuments.* As is usually the case, the integuments begin their development very early as two annular collars around the base of the primordium of the nucellus, the inner slightly in advance of the outer integument. When the megaspore mother cell is ready for reduction division, the inner integument has already grown past the tip of the nucellus (Fig. 1). It consists of two cell layers except at its tip, where it develops a thick ring of tissue later, which helps to narrow down the endostomium.

The outer integument is thicker and consists of five or more layers of cells. Later it encloses the inner integument completely and takes part in the formation of the narrow micropylar canal. In most ovules the exostomium and endostomium do not lie in a straight line, and the micropylar canal therefore is crooked (Fig. 7).

*Nucellus and embryo sac.* The subepidermal archesporial cell which becomes evident at an early stage, divides by a periclinal wall to form a small parietal cell and a megaspore mother cell. The latter enlarges rapidly and becomes embedded under several (four to six) layers of nucellar cells, formed by periclinal divisions of the nucellar epidermis under the micropyle, and of the parietal cell (Figs. 3, 5). All these nucellar cells also divide anticlinally to keep pace with the enlarging megaspore mother cell.

When the megaspore mother cell is ready for reduction division, it is long and narrow and about one quarter the length of the ovule. After reduction division a row of four megaspores is formed. The chalazal one develops into



Figs. 1–10.—*Lanaria plumosa*, longitudinal sections through the developing ovule. Fig. 1, longitudinal section of ovary chamber showing ovule with megaspore mother cell, × 50; 2, young nucellus after division of the archesporial nucleus, and before cytokinesis between the two daughter nuclei, × 350; 3, young nucellus with megaspore mother cell under a 2-layered nucellar epidermis and a parietal cell which had divided anticlinally, × 350. 4, row of four megaspores after reduction division, × 350; 5, functional megaspore enlarging while the others degenerate, × 350; 6, developing embryo sac with four nuclei, × 350; 7, ovule with mature embryo sac, × 50; *ob*, obturator; 8, 9, mature embryo sac showing two synergids, secondary nucleus and two of the antipodal cells in fig. 8, and the egg cell in fig. 9, × 250; 10, antipodal cells, × 250.

an embryo sac, while the other three degenerate (Figs. 4, 5). The nucleus of the chalazal megaspore undergoes three divisions and forms a normal 8-nucleate embryo sac which, when ready for fertilization, contains an egg cell, two synergids, a secondary nucleus and three small antipodal cells (Figs. 8–10). It is inversely pear-shaped, with a narrow projection at the base in which the antipodal cells lie. The latter degenerate slowly after fertilization.

While the embryo sac develops, the adjacent nucellar cells against its upper half degenerate, so that the mature embryo sac has its tip against the cell complex derived from the nucellar epidermis, which forms a small nucellar cap (Fig. 6). The cells derived from the parietal cell have therefore disintegrated. Along its side the embryo sac is covered by a one-layered nucellar epidermis and the disintegrated remains of other nucellar cells. At its base, however, the nucellus is still massive.

Fertilization was not observed, nor the entrance of the pollen tube into the ovule.

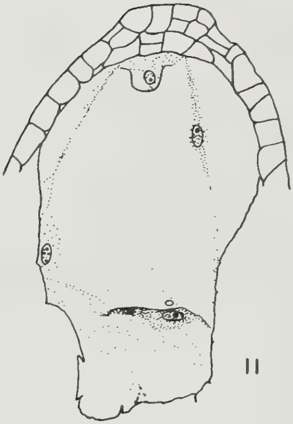
After fertilization the embryo sac enlarges so rapidly that the basal nucellar tissue is often split towards the chalaza. Most of this nucellar tissue is gradually absorbed, the embryo sac forming one to three shallow projections into it (Figs. 11–13). Absorption of this tissue is stopped by a zone of thicker-walled cells with irregular thickenings in the base of the nucellus.

The nucellar cap at the top remains intact for some time, but just below it part of the one-layered nucellar epidermis is now absorbed, so that the sac here touches the inner integument. Along the lower half of the embryo sac the nucellar epidermis remains intact and is still to be seen in the nearly ripe seed.

Only one of the six ovules develops into a seed and the others degenerate. The causes of this degeneration are unknown. Occasionally it starts before the flower opens, and such embryo sacs are narrow and shrivelled. Usually, however, it sets in after fertilization, as often four or five of the ovules in an ovary reach the stage of endosperm development where about four free endosperm nuclei are present.

Other abnormalities are rare. One young ovule was observed with two nucelli, separated by a single inner integument and enclosed in an outer integument common to both. In a few cases three ovules were seen in an ovary chamber instead of two.

*Endosperm.* Although the first division of the primary endosperm nucleus has not been observed, it is probable that the endosperm development is of the helobial type. Young stages with four, eight and sixteen endosperm nuclei show half of these collected in a dense mass of cytoplasm near the base of the embryo sac and cut off from the others by a very thin membrane. This basal endosperm chamber often develops obliquely above the antipodal cells and nearer the side of the raphe, in a slight hollow (Figs. 11–13).



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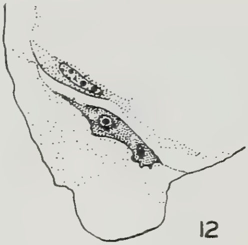

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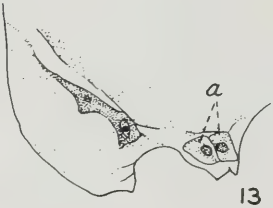

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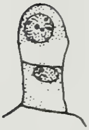

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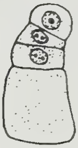

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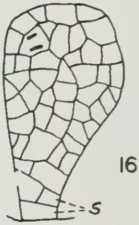

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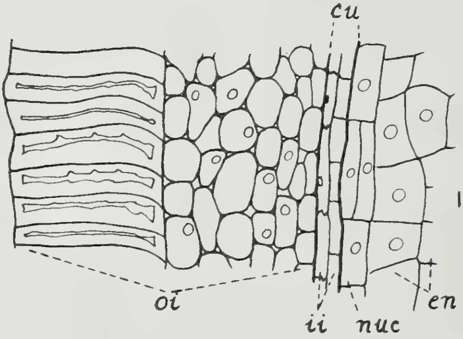

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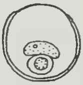

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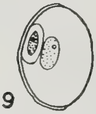

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FIGS. 11–17.—*Lanaria plumosa*, sections through developing seed. Fig. 11, embryo sac after fertilization, with zygote, basal endosperm chamber and several endosperm nuclei, × 200; 12, 13, consecutive sections through basal endosperm chamber, × 200; *a*, antipodal cells; 14, two-celled proembryo, × 350; 15, four-celled proembryo, × 350; 16, still undifferentiated young embryo, × 200; *s*, suspensor; 17, developing seed coat in lower half of seed, × 200; *cu*, middle and inner cuticular layers; *en*, endosperm cells; *ii*, inner integument; *oi*, outer integument; *nuc*, nucellus.

FIGS. 18, 19.—Sections of young pollen grain, showing vegetative nucleus and generative cell, × 600. Fig. 18, cross section; 19 longitudinal section.

At this stage the antipodal cells are still visible (Fig. 13). They disintegrate slowly somewhat later. Directly below them is a small group of resistant nucellar cells which remain small in size, whilst the other nucellar cells adjoining them first enlarge to keep pace with the growing embryo sac, and later get torn and disintegrate.

It was found extremely difficult to make good microscopical preparations of young endosperm stages. The probable reason for this is that the embryo sac enlarges so rapidly and is possibly so flaccid that good fixation is next to impossible. The embryo sac in this stage always shows extreme plasmolysis, and part of the young endosperm layer is often torn away from the embryo sac wall (Fig. 11).

The nuclei in the upper endosperm chamber divide repeatedly and lie in a single layer in the thin layer of peripheral cytoplasm. A large vacuole occupies the centre of the embryo sac.

Cell wall formation in the embryo sac takes place late, when the seed has already reached its full size. At this stage there are probably more than a hundred free endosperm nuclei present, still lying in a single layer in the peripheral cytoplasm. After formation of cell walls, the embryo sac rapidly fills up with thin-walled endosperm tissue which at first contains starch, and later protein and oil.

The basal endosperm chamber has dense cytoplasm and several nuclei. No cell wall formation takes place here. It occupies a slight hollow in the nucellus. This is so shallow that it cannot be rightly termed a haustorium.

*Embryo.* Only the initial stages of the development of the proembryo were seen. Before cytokinesis occurs in the endosperm the zygote divides transversely (Fig. 14). Two further transverse divisions occur, so that a four-celled proembryo is formed with the four cells in a row (Fig. 15). The lower cell is larger than the others and forms a short suspensor. Later stages show that the suspensor remains small and consists of only a few cells, one basal and two above the basal cell (Fig. 16). It is uncertain whether the two upper suspensor cells have been formed by division of the basal or second cell of the four-celled proembryo. The nucellar cap to which the suspensor is attached, gradually disappears.

In the ripe seed the slightly curved embryo is differentiated, and about one half the length of the endosperm tissue. It lies embedded loosely in the endosperm, except for the root tip which projects into a cavity under the seed coat near the micropyle.

*Seed coat.* The seed coat is smooth, black, hard and brittle, and is formed mainly from the outer integument (Fig. 17). Its outer epidermal cells are palisade-shaped with thickened cell walls, giving at first a cellulose reaction. Later these cells turn brown and then black, but just before this stage the middle lamellae stain red with Sudan III, indicating the presence of a suberin-like substance. The black colour of the older cells prevented more microchemical tests being made.

The remainder of the outer integument consists of five or more layers of rounded parenchymatous cells with intercellular spaces, large vacuoles, and thick layers of peripheral cytoplasm containing starch. The inner epidermis of this integument remains small-celled and thin-walled.

Except at its thickened tip the inner integument still consists of only two cell layers which have remained thin-walled. The cells of its outer layer are large and flattened, with folded anticlinal walls, and with very little protoplasm. The cells of the inner layer are somewhat smaller, show no compression, and are rich in protoplasmic contents which take up much haematoxylin. The protoplasm also shows the presence of protein, with Millon's reagent.

The seed coat has three thin cuticular layers: on the outside, between the two integuments, and the third inside the inner integument. Inside the latter there is in the upper half of the seed a cellulose layer probably formed from cell membranes of the disintegrated nucellus. A layer of nucellar cells persists in the lower half of the almost ripe seed (Fig. 17).

At the micropyle the outer integument is unable to keep pace with the enlarging endosperm. The exostomium widens, thus forming a weak spot in the seed coat through which the radicle grows when germinating. This "germ pore" is closed only by the massive parenchymatous tip of the inner integument.

In the chalazal end of the seed is an air space where the basal nucellar tissue has been absorbed by the developing endosperm.

*Germination.* The seeds are dry in February and March. No period of after-ripening is necessary and germination takes place within three weeks. Of ten seeds tested, all germinated.

## DISCUSSION

Table 1 summarizes the important embryological characters of *Lanaria* and genera of the tribes Haemodoreae and Conostyleae, and the Tecophilaeaceae, a family re-established by Hutchinson, to include the Conanthereae of Bentham and Hooker and the Cyanastraceae of Engler & Prantl's system. The genera mentioned are the only ones in these groups whose embryological characters have been worked out. All the genera have a similar early embryo sac development. *Lanaria* agrees in its embryological characters more closely with the genera of the Tecophilaeaceae than with those of the Haemodoreae and the Conostyleae, the tribes to which it has been assigned. It differs from these two tribes in pollen development, character of the tapetum, ovule shape, size of antipodal cells, thickness of outer integument, and in the presence of an obturator near the micropyle.

It agrees with the genera of the Tecophilaeaceae—and especially with *Odontostomum*—in pollen development, absence of an amoeboid tapetum, early ovule development, ovule shape, position and number, and with *Odontostomum* and *Cyanastrum* in the presence of an obturator. The only point in which it differs from all three genera of the Tecophilaeaceae is in the width of its embryo sac. As the presence of an embryo sac haustorium has been investigated in only four of the eight genera, this character is left out of consideration.

TABLE I.

Embryological characters of *Lanaria* and genera of the Haemodoreae, Conostyleae and Tecophilaeaceae.

| | HAEMODOREAE | | | CONOSTYLEAE | TECOPHILAEACEAE | | | LANARIA |
|---|---|---|---|---|---|---|---|---|
| | Wachendorfia | Dilatris | Xiphidium | Anigosanthus | Odontostomum | Cyanella | Cyanastrum | |
| Amoeboid tapetum .. | + | + | + | + | 0 | 0 | 0 | 0 |
| PMC .. .. .. | succ. | succ. | succ. | succ. | sim. | sim. | sim. | sim. |
| Generative cell .. .. | dist. | dist. | | | prox. | prox. | prox. | prox. |
| Parietal cell .. .. | + | + | + | + | + | + | + | + |
| Megaspores .. .. | 4 lin. | 4 lin. | 4 lin. | 4 lin. | 3 lin. | 4–3 lin. | 3 lin. | 4 lin. |
| E.s. development .. | NT | NT | NT | NT | NT | NT | NT | NT |
| Form of e.s. .. .. | narrow | wide | | wide | narrow | narrow | narrow | wide |
| Antipodal cells .. | large | large | | large | | small | small | small |
| Endosp. development | He | He | | | prob. He | Nu | prob. Nu | He |
| E.s. haustorium .. | + | + | | | | + | | 0 |
| Outer integ. .. .. | 2 lay. | 2 lay. | | prob. 2 lay. | thick | thick | thick | thick |
| No. of ovules .. .. | 1 | 1 | ∞ | ∞ | 2 | ∞ | 2 | 2 |
| Form of ovules .. | hemi. | orth. | orth. | orth. | ana. | ana. | ana. | ana. |
| Ovule position .. | down. | down. | ± down. | ± down. | apotr. | sideways | apotr. | apotr. |
| Obturator .. .. | 0 | 0 | 0 | | + | 0 | + | + |
| Authority .. .. | Dellert 1933<br>De Vos 1956 | De Vos 1956 | Stenar 1938 | Stenar 1927 | Cave 1952 | De Vos 1950 | Fries 1919<br>Nietsch 1941 | present |

Abbreviations used: *ana.*, anatropous; *apotr.*, apotropous; *dist.*, distal; *down.*, ovule with micropyle directed downwards; *endosp.*, endosperm; *e.s.*, embryo sac; *hemi.*, hemitropous; *He*, helobial; *lay.*, layers of cells; *lin.*, linear; *no. of ovules.*, i.e. per ovary chamber; *NT*, normal type; *Nu*, nuclear; *orth.*, orthotropous; *PMC*, pollen mother cells; *prox.*, proximal; *sim.*, simultaneous formation of pollen grains in PMC; *succ.*, successive formation of pollen grains. Symbols: +, present; 0, absent.

In seed structure, however, *Lanaria*, *Cyanella* and *Cyanastrum* differ considerably. The seed of *Cyanastrum* has food-storing chalazosperm probably developed from chalazal tissue outside the vascular bundle, no endosperm and a large well-developed embryo (Fries 1919, Nietsch 1941). *Cyanella* and *Lanaria* have well-developed endosperm and differentiated, but small embryos, with polyembryony occurring in Cyanella, but no chalazosperm. In *Cyanella*, furthermore, the chalazal tissue changes into a dry appendage in the ripe seed. No such development takes place in *Lanaria*. The development of the *Odontostomum* ovule after fertilization has not been investigated.

Erdtman (1952) found that pollen structure also points to the fact that *Lanaria* stands closer to the Tecophilaeaceae than to the Conostyleae. He states (p. 46): "It is doubtful, however, whether *Lanaria* and *Lophiola* should be placed in the same tribe as the pollen morphologically very different Australian genera *Anigozanthos*, *Blancoa*, *Conostylis* and *Tribonanthes*. As to size and maybe also exine stratification *Lanaria* and *Lophiola* have more characters in common with Hypoxidoideae-Conanthereae"—i.e. the Tecophilaeaceae—"than with Haemodoraceae sensu Pax".

Certain groups of the Liliaceae (the subtribe Asphodelinae, tribe Aloineae, and genus *Tofieldia*) and the genus *Ixiolirion* of the Amaryllidaceae, widely separated in taxonomic systems, show the same combination of embryological characters as *Lanaria* and genera of the Tecophilaeaceae, viz. simultaneous development of cell walls in the pollen mother cells, proximal position of the generative cell, and in the ovule: presence of a parietal cell, normal type of embryo sac development, helobial endosperm development, absence of an embryo sac haustorium and presence of an aril (Cave 1953, Schnarf and Wunderlich 1939, Seelieb 1924, Stenar 1924). According to Cave and to Schnarf and Wunderlich the Asphodelinae and Aloineae are undoubtedly related.

The problem is whether all these groups showing a similar embryological development are related, or whether the set of embryological features found here, evolved more than once in a number of unrelated groups—this seems hardly possible. In other words, are embryological characters of greater importance than adult characters in indicating relationships? It has been suggested that the internal structure of a flower (and therefore its embryological features) must be more conservative than the external, being less amenable to environmental influence, and that such characters are of special value in judging the proper position of certain doubtful groups (Maheshwari 1945). It must be left to the future to decide to what extent the relationships between the abovementioned groups, indicated by a similar early embryological development, should be reflected in their classification.

Anatomical investigations have been carried out on *Lanaria* and allied genera by Schulze (1893), Schmidt (1891), Scharf (1892) and Solereder (1917), but are not conclusive. Schulze found that the genera of the Conanthereae he studied have no subsidiary cells to their stomata, but that they are present in the Haemodoreae and Conostyleae. This indicates that the Conanthereae are not closely related to the two latter groups. In *Lanaria* and *Lophiola* he found subsidiary cells hardly or not distinguishable from the thin-walled epidermal cells. In *Cyanastrum* subsidiary cells are present (Solereder).

*Lanaria* has trichomes similar in structure to those of *Anigosanthus* and *Conostylis*, while the Conanthereae are glabrous, except for *Cyanella capensis* which has short protuberances on the leaf margins (Schulze). On the other hand, *Lanaria*, *Lophiola*, *Tribonanthes* and *Phlebocarya* disagree in phloem structure from the rest of the Conostyleae, according to the same author.

Anatomically *Lanaria* and *Lophiola* have characters in common, and this indicates that the two genera might be related. The similar pollen structure also points this way. Unfortunately the embryological development of *Lophiola* has not been investigated. Anatomical evidence has not been of help so far in deciding the further relationships of *Lanaria*. It has some anatomical characters in common with the Conostyleae and others with the Conanthereae (Tecophilaeaceae).

The conclusion that can be reached from a knowledge of the embryology of *Lanaria* and allied genera, is that its position in present classifications is probably not correct. Its embryological development indicates a closer relationship with genera of the Tecophilaeaceae (and a few other groups of the Liliaceae and Amaryllidaceae at present widely separated in orthodox taxonomic systems) rather than with the Haemodoreae or the Conostyleae, the tribes to which it has been assigned.

More embryological work on related genera, e.g. *Lophiola*, *Phlebocarya*, and genera of the Tecophilaeaceae is necessary to determine Lanaria's nearest relations.

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